Diversity and Conservation of Neotropical Mammals

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Glossary

Adaptive radiation The evolution of ecological and phenotypic diversity within a rapidly multiplying lineage.
Ecoregion A large unit of land or water containing a distinct assemblage of natural communities and species.
Endemic Any taxon (e.g., species, genus, family, order) confined to a particular region.

GABI The Great American Biotic Interchange was the major exchange of land mammals between South and North America after the formation of the Isthmus of Panama, about 2.7 million years ago.
Rapoport effect A pattern where the size of a species' geographic range increases toward higher latitudes.

Introduction

The characteristics and biogeography of Neotropical mammals have been the focus of copious literature. The interest in the Neotropical region lies in its long isolation during the Cenozoic Era (Age of Mammals), particularly in South America, and the extensive radiations that led to a remarkable fauna within a context of heterogeneous topography and extraordinary diversity of ecoregions. The foundations of the knowledge of Neotropical mammals were laid in the voyages of Christopher Columbus in 1492, naturalist expeditions up into the nineteenth century, as well as by pioneers of South American mammal paleontology (Hershkovitz, 1987).

Neotropical Land Mammals: History of Place and Lineages

Among the most prominent contributions to Neotropical mammal biogeography are the studies of Simpson (1950, 1980), Hershkovitz (1958, 1972), Cabrera and Yepes (1960), Patterson and Pascual (1972), Reig (1981), Webb and Marshall (1982) and Mares and Genoways (1982), among others.

The evolutionary history of Neotropical mammals (that is, the history of lineages) should be framed within the dynamic history of place (i.e., changes in geography, geology, climate, and environmental characteristics; Lomolino *et al.*, 2010). Thus, major paleogeographic events were the Division of Pangea into Gondwana and Laurasia, the breakup of Gondwana (into South America and Africa) during the upper Cretaceous, the isolation of South America as an "island continent" for more than 100 million years, throughout much of the Tertiary, the emergence of the Panamanian land bridge, and the rise of the Andean Cordillera.

Chronologically, the immigration of recent land mammals into the Neotropical Region can be divided into three distinct faunal strata (Simpson, 1980; Webb and Marshall, 1981) reflecting older and younger faunal contingents. These strata are the result of a fragmentary fossil record, and represent only a general heuristic framework synthesizing the history of the Neotropical mammal fauna (Figure 1).

Prior to the first stratum, a protohorofauna (i.e., a Mesozoic Gondwanian fauna made up of mammal-like reptiles and true mammals from which part of the following fauna might have taken their origin; Reig, 1981) was present or had evolved in South America from Western Gondwanian or Laurasian groups; some Neotropical lineages of Stratum 1 may have originated from them (Reig, 1981). Stratum 1 is made up of the ancient autochthonous fauna of the early Cenozoic, and includes the living armadillos, giant anteater, marsupials, and various diverse and now-extinct groups of autochtonous ungulates. Stratum 2 represents the allocthonous lineages present in early Oligocene that includes the caviomorph rodents and primates (the origin of both groups are contentious, but they are probably African). The Stratum 3 corresponds to the young taxa, associated with the emergence of the Panamanian land bridge, and consequently, the large-scale experiment of faunal interchange known as the Great America Biotic Interchange (GABI), during late Pliocene, at about 3 million years ago. Among the mammal invaders from the North American stock are the procyonids (coati and racoon), vespertilionid and molossid bats, skunks, peccaries, cricetid rodents, mastodons, camelids, tapirs, bears, horses, deer, dogs, weasels, cats, leporids and squirrels (Marshall, 1988).

There is still debate regarding these phases, specifically the time and place of entry of some lineages. An example is the long-standing debate regarding the arrival and diversification of the cricetid field mice in South America, particularly the diverse subfamily sigmodontine with more than 300 species. Although there is a general consensus on North America as the place of origin of this lineage, there is controversy on whether their explosive diversification took place in North or South America. Some authors suggest that it occurred in Central America, and that the subfamily was already taxonomically diverse when they arrived in South America, whereas others suggest that the subfamily underwent a large scale adaptive radiation once in South America. The centers of diversity are now in South America, although many species are distributed into Central America and a few in the southern USA (Marshall, 1988; Steppan, 1996).

The Great American Interchange

The most impressive change in the composition of the South American land mammal fauna began in the late Miocene (Webb and Marshall, 1982). During this period, representation of genera from Stratum 1 (autochthonous ungulates and large herbivorous xenarthrans) declined from 70% to less than 20%.
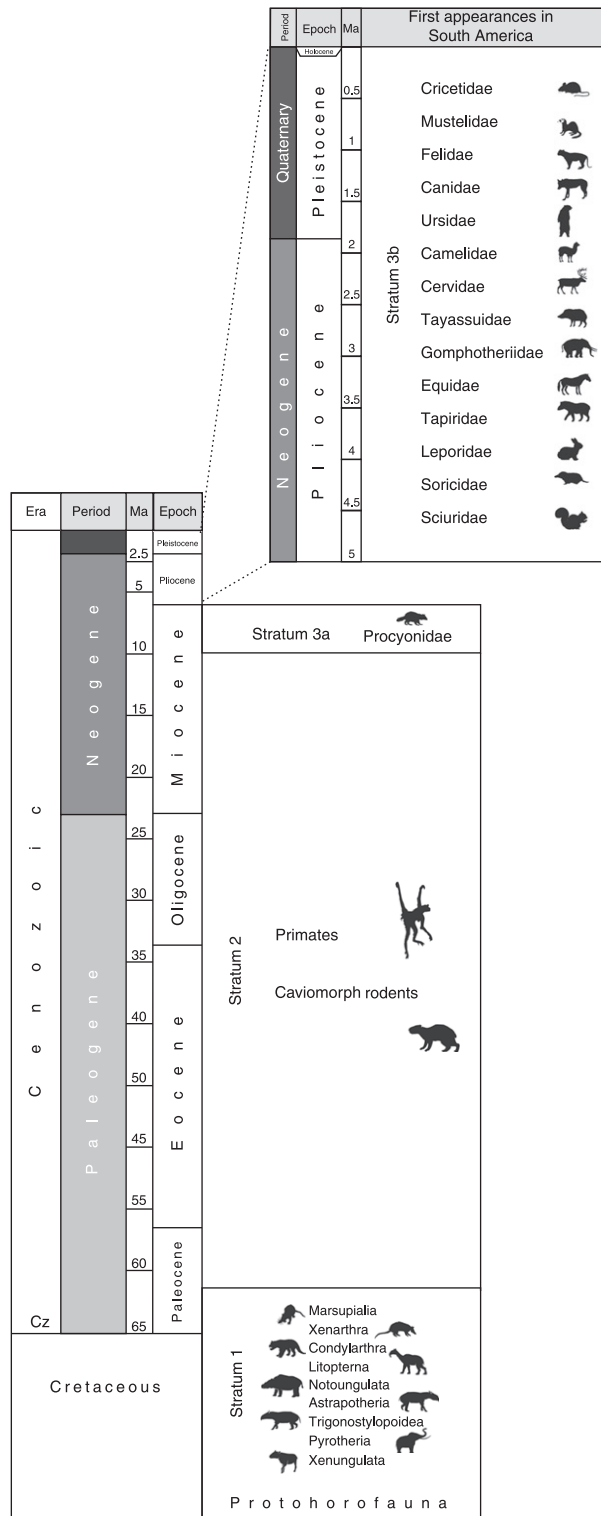
Figure 1   Cenozoic South American land mammal ages and faunal strata.

Concurrently, caviomorph rodents (making up much of Stratum 2) experienced remarkable adaptive radiation into the newly vacant herbivorous niches, ecologically equivalent to mammal groups in other continents (Mares and Ojeda, 1982).

However, the most remarkable episode involved the increase in the diversity of Stratum 3 fauna from 0% to more than 50% of the total genera. At least half of the recent land mammal genera of South America belong to this stratum.

The geological events that took place about 3 million years ago (e.g., tectonic changes and a decrease in sea level) gave rise to the Isthmus of Panama, triggering the GABI. The arrival of the species from Stratum 3 to South America, and a reciprocal faunal interchange with North America, is partly linked to this event. However, some of the mammals of Stratum 3 entered South America before the emergence of the land bridge. During the late Miocene and early Pliocene, island archipelagos may have facilitated waif dispersal (i.e., dispersal across water barriers by island-hopping) across what is now Central America. At the beginning of the Cenozoic, Central America was probably the source area of ancient lineages of marsupials, xenarthrans, and ungulates that dispersed to South America as waif immigrants across the water barrier (Patterson and Pascual, 1972). A successful group that probably arrived as island hoppers in the late Miocene are the sigmodontine rodents (Hershkovitz, 1972; Reig, 1981). At the same time (7–9 million years ago), South American ground sloths entered North America. A summary of the reciprocal land mammal interchange between North and South American is portrayed in **Figure 2**.

A mass extinction, particularly megaherbivores, affected the Neotropical faunal assemblages at the end of the Pleistocene (Martin, 1967; Marshall, 1988). This coincided with the entrance of humans from Asia into North America across the Beringian land bridge at the end of the last glaciation and continued to South America. Earliest human settlements in South America may date back 14,220 years (Dillehay *et al.*, 2008). In the case of North America, there were about 34 extinct genera, whereas in South America the loss of megafauna (i.e., more than 44 kg) reached 52 genera including mastodons, ground sloths, glyptodonts, and the diverse group of native ungulates (Barnosky and Lindsey, 2010).

The megafaunal extinction during the Quaternary period (Late Pleistocene–Holocene) is hypothesized to be the result of synergistic interactions of environmental modifications and hunting, associated with climate change and the dispersal of early humans into the Americas. Although there has been improvement in the dating of extinctions and paleoclimatic reconstruction, the association of human artifacts and megafaunal extinctions are still a matter of active debate (Barnosky and Lindsey, 2010).

The Zoogeographic Region and their Mammals

Biogeographical Limits and Transition Zones

Hershkovitz (1958) defined a zoogeographic region as

> A zoogeographic area, whether Realm, Region, or subdivision thereof, regarded as a faunal district of the earth at a stated time in geologic history. The fauna of a zoogeographic area includes all animals inhabiting that area at the same time irrespective of their place of origin. A zoogeographic boundary between faunal areas is the barrier that prevents a natural and continuous faunal flow from one area to the other. A zoogeographic transition zone is an area on either or both sides of the arbitrarily drawn boundary line between contiguous and contemporaneous faunal areas. Its entire fauna is derived from neighboring areas (1958, p. 584).

Figure 2   The Great American Biotic Interchange and the Central America filter effect. The expansion and retreat of glaciers affected the ecosystem dynamics in Middle America and acted as a filter for the dispersal of certain mammal groups. During the advance of glaciers there was an expansion of the savanna habitats which favored reciprocal dispersal of certain types of fauna to pass through the Isthmus of Panama, whereas during glacier retreats there was an advance of tropical habitats, a contraction of the savanna corridor and consequently a restriction to the dispersal of the savanna faunal groups.

The Neotropical Region was defined by Sclater and Wallace as one of the six major zoogeographical divisions of earth based on their vertebrate assemblages (Sclater, 1858; Wallace, 1876). The region extends from Central America to the southern tip of South America, including continental and oceanic islands, the Bahamas, West Indies, Galapagos, and Malvinas (Falklands). It is subdivided into hierarchically lower divisions known as the West Indian, Brazilian, and Patagonian Subregions.

The delimitation between the Neartic and the West Indian Subregion is an imaginary line across the Gulf of Mexico and the strait of Florida. The West Indian Subregion consists of a chain of islands including the Bahamas, Cuba, and the Grenadines. The Brazilian Subregion extends from Central America and northern South America up to northeastern Argentina. Major topographic features include the Andes extending along the western portion of South America and the Guianian and Brazilian highlands in the northeast and southeast, respectively. Included in its diverse vegetation are rainforests, savannas, mountain meadows, deciduous and evergreen broad-leave forests, and coastal mangroves. The Patagonian Subregion includes Uruguay, most of Argentina (including Malvinas islands), Chile, the highlands of Bolivia and Peru, and the paramos of Ecuador up to the equator. Major topographic and vegetation features include the Pacific coastal desert, the Andes, the vast Patagonian steppe desert, *Nothofagus* beech forests, arid, and semiarid scrublands, savanna and open thornscrub forests, and grassland habitats (Hershkovitz, 1974).

There have been various different biogeographical approaches and methodologies to set the boundaries between the Neartic and Neotropical zoogeographic regions. Some of these proposed limits based on the southern and northern geographic range edges of mammals are synthesized in the inset of Figure 3. Disagreement among these regions are due to different methodologies and taxa analyzed. Thus, the boundary between the Neartic and Neotropical Regions based on the distributional patterns for different taxonomic levels (i.e., families, genera, and species) shows that the southern boundaries of Neartic taxa are located in northern Mexico up to the Mexican Plateau (Escalante *et al.*, 2010). Another quantitative analysis of the distribution of bats in Mexico and Central America (i.e., cells of presence/absence occupancy) found a similar pattern for the southern limits of the Neartic region, with minor differences regarding the extent of the transitional zone (Ortega and Arita, 1998).

The boundaries between biogeographic divisions (referred to as transition zones especially on land), are difficult to determine and are unrealistically portrayed as sharp lines. Instead, these boundaries represent dynamic areas of biotic overlap, active belts of intense faunistic interactions and large-scale population dynamics (Ortega and Arita, 1998; Escalante *et al.*, 2010; Morrone, 2009; Lomolino *et al.*, 2010).

The transition zone between the Brazilian and Patagonian Subregions runs diagonally between southern Ecuador, Peru, Bolivia, and southeastern Brazil, and into Argentina. In

Figure 3   The Neotropical Region and subregions (adapted from Hershkovitz, 1972). The insert map depicts several delimitations of the Neartic–Neotropical transition zone that were proposed by different authors.

northwestern Argentina, the Brazilian Subregion extends like a peninsula (see **Figure 3**) including the southernmost montane cloud forests which stretch to northern South America along the eastern flank of the Andes (Tropical Andes hotspot). Mammal distributions in this transition zone result in a broader transitional area which is roughly congruous with previous boundaries established by Sclater and Wallace as well as the "subtropical line" of Ruggiero *et al.* (1998).

Diversity and Classification of Mammal Groups

The geological history and biotic diversity of the Neotropical Region are the focus of active research, with active discovery of new taxa at various levels. Extant Neotropical mammals represent one quarter of the worlds mammal fauna. Eight of the 20 richest countries in mammals are in the Neotropical Region (Brazil, Mexico, Peru, Colombia, Argentina, Ecuador, Bolivia, and Venezuela, in descending order). However, tabulations of mammal species are imprecise, with new species (particularly marsupials, insectivores, primates, bats, and rodents) being discovered and described rapidly (Patterson, 1994, 2000). New mammal discoveries are particularly significant in South America, especially in areas of high endemism such as tropical biomes (e.g., Central America, eastern tropical Andes, the Amazon basin, and Atlantic forests), and temperate semiarid habitats.

On average, 223 new mammal species are described every 10 years. Of the 62% newly-described New World mammal species in recent years, 93% were from the Neotropical region,

mostly from the tropical and semitropical regions of Mexico and Brazil, the Andes of Colombia, Peru and Ecuador, as well as the temperate areas of Chile and Argentina (Ceballos and Ehrlich, 2009; Reeder et al., 2007).

Of the about 1550 mammal species recently estimated for the Neotropical Region (Solari et al., 2012), 1421 species are from land habitats, and 946 of these (66%) are endemic.

The Neotropical Region has the highest diversity of mammals in the New World, with 15 orders of terrestrial and marine mammals three of which are endemic. The marsupials belonging to the orders Microbiotheria (e.g., monito del monte) and Paucituberculata (i.e., rat and shrew opossums) are mostly restricted to the Patagonian Subregion, whereas the order Pilosa (giant and lesser anteater, and two and three-toed sloths) is restricted to the Brazilian Subregion.

With respect to families, the Neotropical Region has the largest number of endemic families of terrestrial mammals, 29/56. The endemicity ratio (endemic families/number of families) of other biogeographic regions is: Palearic: 1/36; Nearic: 2/31; Afrotropic: 20/58; Indo-Malayan: 8/49, and Australasian: 21/35 (Vaughan et al., 2011).

A General Account of the Neotropical Mammal Fauna

This section provides an overview of the Neotropical mammals. Figure 4 depicts some representatives of these orders and endemic families.

Didelphimorphia – This is an ancient lineage of small to medium-sized marsupials in the Neotropical Region. They occupy a wide diversity of habitats and macroniches (arboreal, scansorial, and semiaquatic; insectivores, frugivores, omnivores, and carnivores). Some genera are *Didelphis*, *Caluromys*, *Glironia*, *Lutreolina*, *Phylander*, *Thylamys*, and *Monodelphis.* All species are endemic to the Neotropical Region, except for the common opossum, *Didelphis virginiana*, which extends its geographic range into the Neartic Region up to Canada.

Paucituberculata – This endemic order of small insectivorous marsupials is confined to South America and is represented by a single family containing the genus *Caenolestes*, *Lestoros*, and *Ryncholestes*. Their distribution extends across Ecuador, Peru, and Bolivia (*Caenolestes*, *Lestoros*), and southern Chile (*Rhyncholestes*).

Microbiotheria – This is a monospecific order with a single family and species, endemic to South America, the small marsupial *Dromiciops australis*. ("monito del monte"). It feeds on larvae, insects, and fruits, and is restricted to the Valdivian temperate rainforest of *Nothofagus* in Argentina and Chile Phylogenetically. it is more closely related to Australian marsupials than to South American ones.

Sirenia – This group is represented by the family Trichechidae, and composed of three species which are endemic to the Amazon and Orinocco basin of the Brazilian Subregion. They are strictly aquatic and herbivorous, and include the manatee (*Trichechus*) and Amazon river dolphins (*Sotalia, Inia*).

Cingulata – This order, along with Pilosa and the marsupials, are among the emblematic "old inhabitants" of the Neotropical region. The order Cingulata includes a diverse suite of armadillos with varying body sizes, ranging from the pink fairy armadillo (100 g) to the giant armadillo (30 kg). Representative genera are: *Dasypus*, *Euphractus*, *Cabassous*, *Priodontes*, *Tolypeutes*, *Chaetophractus*, *Chlamyphorus*, *Calyptophractus* and *Zaedyus*. Armadillos do not occur in the Neartic Region (North America) with the single exception of *Dasypus novemcinctus*, which extends into southeastern United States. They are omnivores that feed on insects, larvae, eggs and fruits.

Pilosa (=Edentata) – This order includes the tree sloths of the genus *Bradypus* and *Choloepus*, and the anteaters (*Tamandua*, *Myrmecophaga*, and *Cyclopes)*. Tree sloths are arboreal folivores, feeding on leaves and buds; they are mostly tropical in their distribution, and occur from Central America to near the Tropic of Capricorn in northern Argentina. Anteaters are terrestrial and semiarboreal and feed on ants and termites.

Primates – Primates are represented by two endemic and one cosmopolitan (Hominidae) families which includes humans, *Homo sapiens.* Neotropical monkeys are mostly tropical forest species and are small to medium size. Among them, the pigmy marmoset, *Cebuella pygmaea* with a body weight of 70 g, is the smallest of the living primates. Neotropical monkeys are arboreal and with a diet of insects, leaves, and fruits. Whether they originated in Africa or Asia is still a matter of debate. Representative genera, many of them highly endangered, include *Cebuella*, *Saguinus*, *Callithrix*, *Leontopithecus*, *Aotus*, *Saimiri*, *Ateles*, *Alouatta*, *Cebus*, among others.

Rodentia – Rodents are represented by four major groups, or suborders: Sciuromorpha, Castorimorpha, Hystricomorpha, and Myomorpha. Of these, the Castorimorpha and Sciuromorpha are of northern origin, and they reach their southern distributional limits in distribution in northern South America and near the Tropic of Capricorn, respectively. Representative genera of Sciuromorpha are squirrels, *Sciurus*, whereas the Castorimorpha is represented by subterranean pocket gophers (*Geomys*, *Orthogeomys*) and spiny pocket mice (*Liomys*, *Heteromys*). The other two suborders, Hystricomorpha and Myomorpha, include the endemic and highly diversified caviomorphs (the South American hystricomorphs) and sigmodontine rodents, respectively, which underwent explosive adaptive radiation in the Neotropics, mainly in South America. These two groups account for more than 550 species, ranging from 12 g to 50 kg (e.g., the largest living rodent, capybara), and occupy a full array of habitats and modes of life. Caviomorph rodents comprise 11 endemic families and some genera are *Galea, Dolichotis, Abrocoma, Ctenomys, Octodon, Tympanoctomys, Spalacopus, Proechimys, Hydrochaeris, Agouti, Dasyprocta, Cuniculus,* and *Coendu,* among the most conspicuous. Representative genera of sigmodontine rodents are: *Isthmomys, Icthyomys, Oryzomys, Thomasomys, Wiedomys, Calomys, Sigmodon, Akodon, Eligmodontia, Phyllotis, Salinomys, Euneomys,* and *Abrothrix*.

Lagomorpha – This order is represented by the family Leporidae (rabbits and hares) and includes the North American cottontail rabbits. In the Neotropical Region it is represented by the genus *Sylvilagus.* Some of these herbivorous mammals have distributions from Central America to northern Argentina and southern Brazil. Other members of this family are represented by the European rabbit (*Oryctolagus*) and European hare (*Lepus*), introduced by humans in the Neotropical region.

Soricomorpha – This order includes the insectivorous shrews which are distributed across Central America, the West Indian Subregion, and barely into the subtropical Andes in northern South America (genus *Cryptotis*). The endemic family

Solenodontidae includes two endangered species of the genus *Solenodon* distributed in Cuba and the Dominican Republic.

Chiroptera – Bats, the second most speciose mammals in the Neotropical Region. Six out of nine families are endemic

here; their feeding niches are highly diversified and include sanguinivores, frugivores, insectivores, carnivores, nectarivores, pollinivores, and piscivores. Representative genera of different families are *Noctilio, Glossophaga, Brachyphylla, Carollia, Tonatia, Desmodus, Vampyrops, Artibeus, Mormoops, Peropteryx, Thyroptera, Natalus, Molossus, Lasiurus,* and *Eumops*.

Carnivora – This is a diversified group of mammals occupying terrestrial, arboreal, aquatic and marine habitats. They are represented by eight families which are widely distributed in the Neotropical Region and include the large and medium-size spotted cats, weasels, skunks, river otters, elephant seal, sea lions, foxes, raccoons, coatis, and the spectacled bear. Representative genera are *Panthera, Felis, Galictis, Conepatus, Lutra, Lontra, Nasua, Potos, Tremarctos, Hydrurga, Mirounga,Arctocephalus,* and *Otaria*.

Perissodactyla – This ungulate group possess an enlarged middle digit on the anterior and posterior limbs, hence the name of odd-toed ungulates. The order is represented by three species of tapirs in the genus *Tapirus*, among the largest terrestrial mammals in the Neotropical Region. They occur from Central Mexico to northern Argentina and feed on grasses and fruits. They are mostly distributed in tropical and gallery forests, forested foothills, tropical Andean paramos, and riverine environments.

Artiodactyla – These are the even-toed ungulates. In the Neotropical Region this order is represented by three families. Representative genera are *Tayassu, Lama, Vicugna, Pudu, Mazama* and *Ozotoceros*, and include the peccaries, guanacos, vicuñas, pampas deer and brocket deer, and pygmy pudu deer. Their diet is mostly herbivorous (deer and camels) and omnivorous (peccaries) and they are distributed from southern North America (collared peccaries; genus *Tayassu*) to the southern tip of South America (guanacos).

Cetacea – A group of strictly marine mammals that is distributed worldwide and represented by whales, dolphins, and porpoises; they feed on fish and small crustaceans. Representative genera are *Pontoporia, Delphinus, Lagenorhynchus, Orcinus, Tursiops, Phocoena, Mesoplodon, Physeter, Balaenoptera Megaptera,* and *Balaena*.
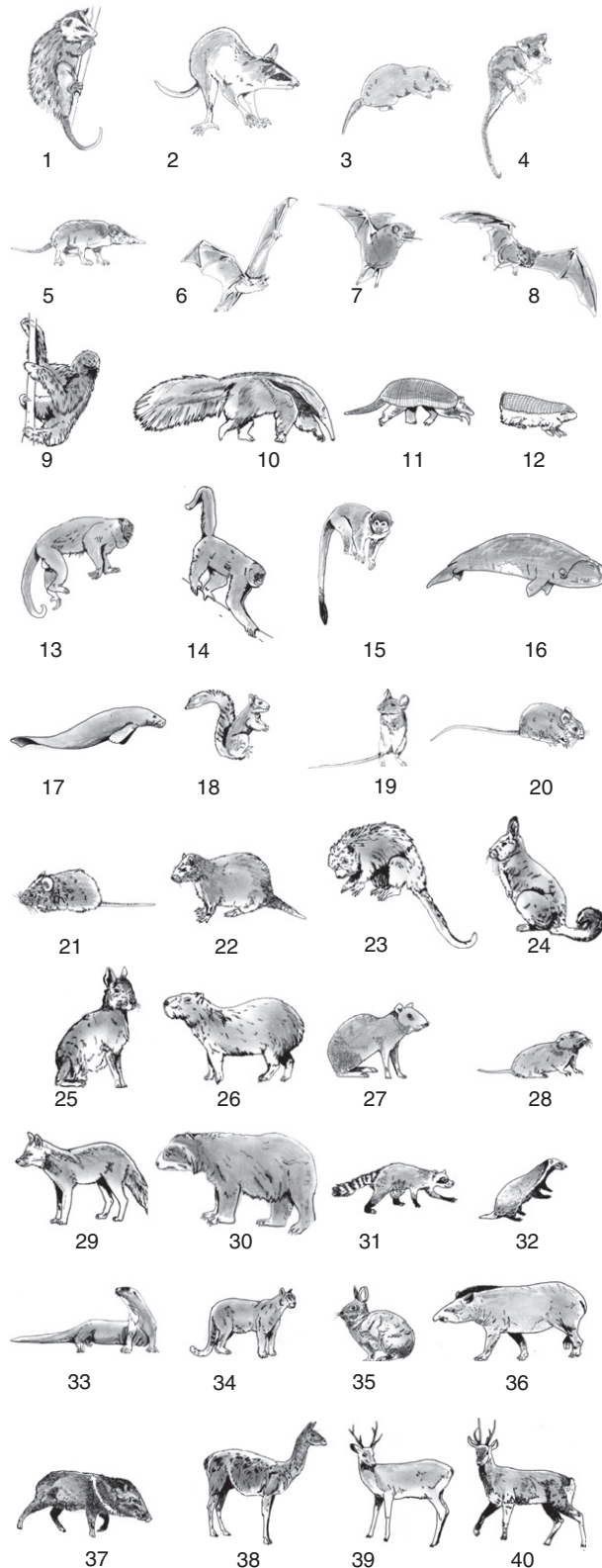

Figure 4 Representative orders and species of Neotropical mammals. Didelphimorphia: (1) *Didelphis albiventris*; (2) *Metachirus nudicaudatus*; Paucituberculata: (3) *Rhyncholestes raphanurus*; Microbiotheria: (4) *Dromiciops australis*; Soricomorpha: (5) *Solenodon cubanus*; Chiroptera: (6) *Noctilio leporinus*; (7) *Glossophaga soricina*; (8) *Eumops auripendulus*; Pilosa: (9) *Bradypus torquatus*; Cingulata: (10) *Myrmecophaga tridactyla*; (11) *Priodontes maximus*; (12) *Chlamyphorus truncatus*; Primates: (13) *Alouatta palliate*; (14) *Lagothrix flavicauda*; (15) *Saimiri sciureus*; Cetacea: (16) *Eubalaena australis*; Sirenia: (17) *Trichechus manatus*; Rodentia: (18) *Sciurus ignitus*; (19) *Eligmodontia typus*; (20) *Oryzomys longicaudatus*; (21) *Akodon molinae*; (22) *Capromys pilorides*; (23) *Sphigurus mexicanus*; (24) *Lagidium viscacia*; (25) *Dolichotis patagonum*; (26) *Hydrochoerus hydrochaeris*; (27) *Dasyprocta punctata*; (28) *Ctenomys talarum*; Carnivora: (29) *Dusicyon culpaeus*; (30) *Tremarctos ornatus*; (31) *Procyon cancrivorus*; (32) *Lyncodon patagonicus*; (33) *Pteronura brasiliensis*; (34) *Puma concolor*; Lagomorpha: (35) Sylvilagus brasiliensis; Perissodactyla: (36) *Tapirus terrestris*; Artiodactyla: (37) *Tayassu tajacu*; (38) *Lama guanicoe*; (39) *Ozotoceros bezoarticus*; (40) *Hippocamelus antisensis*.

Biogeographical–Macroecological Patterns

Patterns of Species Richness

The distribution and diversity of Neotropical mammals have been analyzed for many groups utilizing different biogeographic approaches, from the continental scale (e.g., Mesoamerica and South America) to regional biomes and countries. The inverse relationship between richness of Neotropical land mammals and latitude is similar to that found for many other taxa of plants and animals. One of the first to quantify and explain this large-scale pattern of decreasing species richness from low equatorial latitudes to high temperate latitudes for the mammals of the Nearctic region (North America) was Simpson (1964). This pattern has been analyzed and corroborated for the New World mammals and several taxa such as marsupials, bats, caviomorph rodents and carnivores, among others. The highest concentration of terrestrial (nonvolant) mammals in South America, is found along the eastern Andes of Bolivia, Peru and Ecuador, the Amazon Basin, and the Atlantic Rainforests of Brazil (Mares and Ojeda, 1982; Kaufmann, 1995; Ruggiero, 1994; Tognelli and Kelt, 2004 (Figures 5 and 6).

Although researchers agree on the generality of this latitudinal trend, there is considerable debate over its causes (i.e., historical, ecological, climatic stochastic and integrative hypotheses, Chown et al., 2004; Lomolino et al., 2010). For example, the large area of tropical South America has been suggested to explain diversity of biotas at both continental and island scales (Mares and Ojeda, 1982; Rosenzweig, 1995; Rosenzweig and Sandlin, 1997). However, the latitudinal diversity gradient for New World marsupials and bats could be explained by a null model (i.e., the pattern in species richness could be a consequence of stochastic mechanisms independent of any particular factor or environmental gradient), up to some extent (Willig and Lyons, 1998). However, further analysis of the joint effects of latitude and area has shown that latitude is the dominant factor which explains greater than 50% of the variation in mammal species richness. This relationship is independent of area, which contradicts the explanations involving area as one of the major drivers in species diversity (Kaufmann, 1995; Lyons and Willig, 1999).

Regardless of this debate, global trends of latitudinal diversity in mammals are driven by a combination of factors, including energy availability, topographic complexity, and area, among others. As a result, land mammal species richness peaks toward the equator, in conjunction with primary productivity, whereas richness of marine mammals peaks at approximately 40° N and S, corresponding to belts of high oceanic productivity (Schipper et al., 2008). In the particular case of South America, energy input converted into larger primary productivity and then translated into greater resources available to consumers, explains a large part of the latitudinal diversity gradient (Tognelli and Kelt, 2004). Other variables such as habitat heterogeneity, topographic variability, climate, and number of ecosystems, are less important in determining mammalian species richness at this continental scale of analysis, although they are relevant in explaining mammal diversity at regional and local scales. Furthermore, despite corroboration of this relationship, some of the reported differences between results on large scale latitudinal gradients are
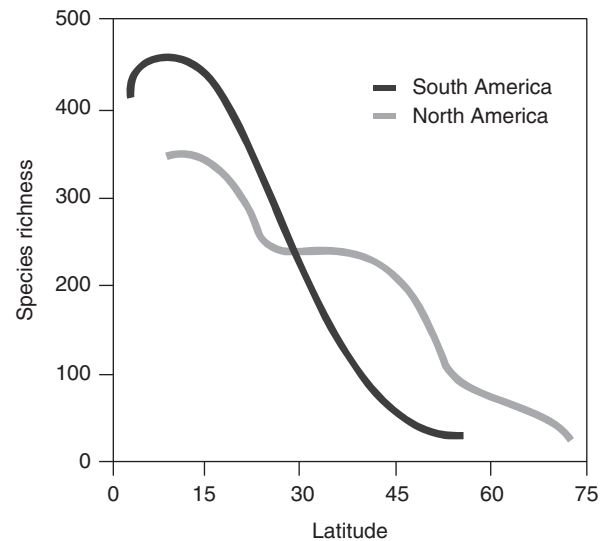

Figure 5 Patterns of latitudinal diversity in North and South American mammals.

likely due to the utilization of different databases, methodology, scale of analyses, number and type of taxa involved, and statistical models (Kaufmann and Willig, 1998; Tognelli and Kelt, 2004).

In general, ongoing research regarding the explanation of latitudinal gradients in species diversity is shifting from the need to find a unique driving factor to a more integrative approach of hypotheses and theories combining several factors (Lomolino et al., 2010).

Detailed reviews and summaries of current knowledge and compelling hypotheses for a latitudinal gradient in species richness have been provided by Rosenzweig (1995), and Lomolino et al. (2010).

Areographic Patterns and Ecogeographic Rules

Sizes and shapes of geographic ranges are influenced by the topography of the region. Thus, South American mammal geographic ranges become more asymmetrical (relative to a circle) toward the west as a result of the topographical complexity of the Andes. The most widespread species are located in eastern Brazil, whereas the most restricted species are associated with the Andes. The major contrast in South American mammal range sizes therefore occurs in an east–west direction, along the boundaries between the Guayana-Brazilian and Andean-Patagonian Subregions, in accordance with the classical zoogeographical delimitations (Ruggiero et al., 1998).

The increase in body sizes from the equator toward the Poles (toward high, colder latitudes) is a generalized pattern known as Bergmann's Rule (Lomolino et al., 2010). However, there is marked contrast between patterns among the mammal faunas of the Nearctic (North America) versus the Neotropical Region. Although in the Nearctic Region body size is negatively correlated with temperature, increasing toward high latitudes, in the Neotropical Region there is a positive correlation with temperature such that mammals are larger in warmer tropical latitudes and smaller in the mountainous Andean regions.
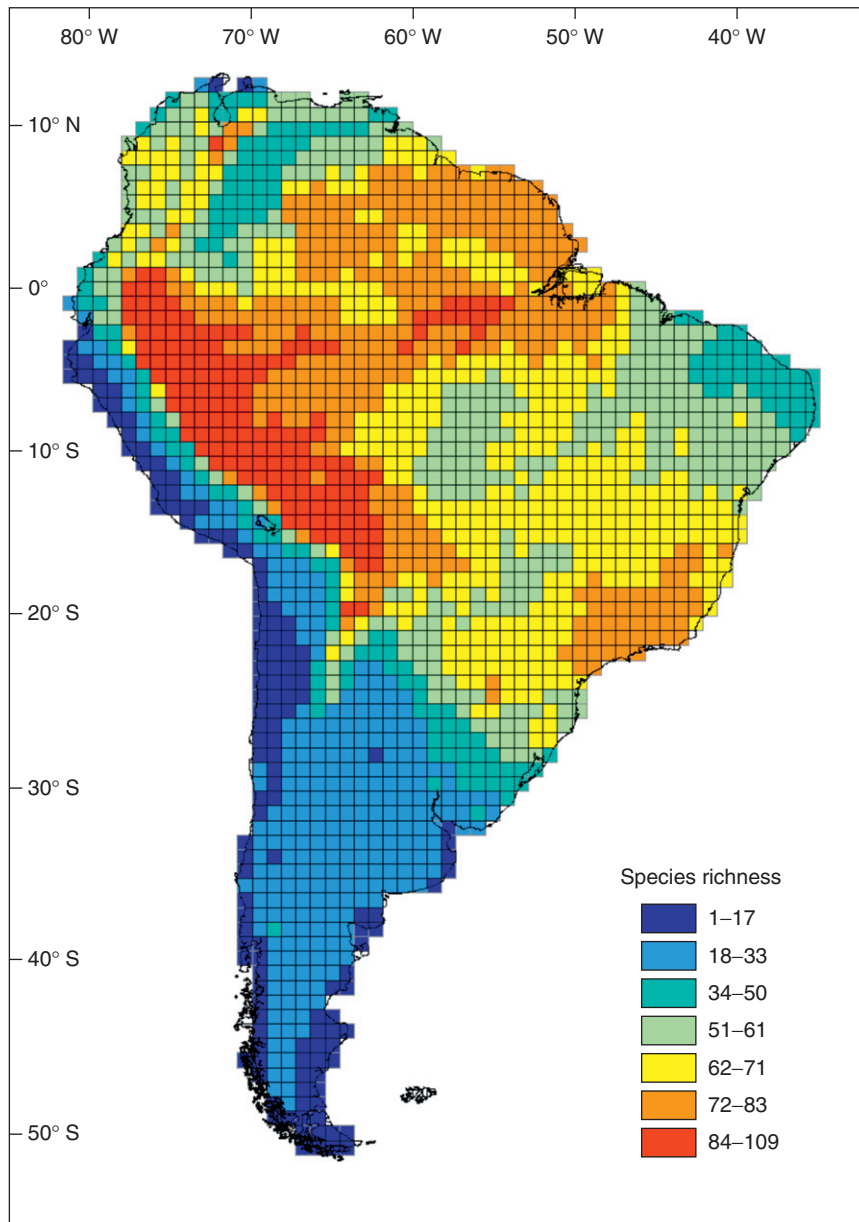
Figure 6 Patterns of diversity of South American nonvolant mammals.

A suggested explanation for this is that reduced habitat in mountains produced an area effect resulting in fewer large-sized mammals (Rodriguez et al., 2008; Ruggiero, 1994).

Another ecogeographic rule known as the Rapoport Rule (Stevens, 1989), states that the latitudinal ranges of species tend to increase toward higher latitudes. An explanation for this trend is that greater climate seasonality and variability at high latitudes exerts a selective effect promoting greater flexibility and larger geographic ranges of species. In South America, Rapoport's rule is consistent with observed patterns only for carnivores and primates; support is less clear for caviomorph rodents, marsupials, and artiodactyls. Anteaters, tree sloths, and armadillos show the opposite trend, with their geographic ranges decreasing toward higher latitudes Ruggiero (1994). Overall, contrary to the Neartic Region, there is a lack of evidence regarding increases in geographic ranges toward higher latitudes in South America. This could be associated with the fact that there is less temperature variation in the southern hemisphere, compared to the northern hemisphere (Chown et al., 2004).

Mammal Conservation and Major Threats

As a result of the Neotropic's high mammal diversity and endemicity, their conservation is a key issue in the region. Roughly, of the 76 world mammal species that have become extinct in the past 500 years (http://roboconsumer.word-press.com/2007/09/23/extinct-mammals/) 34 (45%) occurred in the Neotropical Region.

One of the first extinct canids was the Malvinas (or Falkland Islands) fox (*Dusycyon australis*), an event already predicted by Darwin (1860) during the voyage of the Beagle

> "…As far as I am aware, there is no other instance in any part of the world, of so small a mass of broken land, distant from a continent, possessing so large an aboriginal quadruped peculiar to itself. Their numbers have rapidly decreased; they are already banished from that half of the island which lies to the eastward of the neck of land between St. Salvador Bay and Berkeley Sound. Within a very few years after these islands shall have become regularly settled, in all probability this fox will be classed with the dodo, as an animal which has perished from the face of the earth." (Charles Darwin, The Voyage of the Beagle, 1860, entry for March 16th, 1834)

Most of these extinctions were the result of a combination of factors, including ecological attributes (i.e., habitat or diet specialists), coupled with restricted insular distributions (e.g., Haiti, Dominican Republic, Cuba, Puerto Rico, and Malvinas), and anthropogenic factors affecting mammals worldwide, such as overhunting, habitat destruction, and the introduction of alien species (e.g., rats, cats, and dogs) (Schipper *et al.*, 2008). In the long term, global climate change is becoming a matter of increasing concern (MacLean and Wilson, 2011).

About 52% of mammals worldwide whose population trends are known, appear to be contracting their geographic ranges and declining their populations (Schipper *et al.*, 2008). At the scale of countries, a detailed overview of the diversity and major conservation problems facing the mammal fauna of the Neotropical Region, such as deforestation, hunting, wildlife trade, and introduction of exotics, was provided by Ceballos and Simonetti (2002). Habitat loss and fragmentation from extensive deforestation is common throughout the Neotropics. In South America, most losses of mammals are associated with cattle grazing and intensive agricultural activities, particularly in the Pampas region (Argentina), Mata Atlantica (Brazil), and coastal areas of Ecuador and Peru. These disturbances are particularly relevant in mammals of temperate South America because of its characteristic high number of endemisms and small geographic ranges (Ceballos and Ehrlich, 2002; Schipper *et al.*, 2008; Lamoreux and Lacher, 2010).

Subsistence hunting, and particularly faunal commercialization, are important threats to mammal populations in the Neotropical Region (Ojeda and Mares, 1982; Iriarte and Jaksic, 1986; Robinson and Redford, 1991) **(Table 1)**. An example of the commercial scale of mammal exploitation is provided by official statistics from the trade of wildlife products (e.g., skins, hides, fur, and meat) from Argentina which represented more than 30 million dollars during 1976–1979 (Ojeda and Mares, 1982). Between 1972 and 1979, Argentina exported 22 million mammals. Despite international agreements on the conservation of marine mammals, the dominant threats are harvesting and accidental mortality, (Schipper *et al.*, 2008).

Biological invasions are another threat to Neotropical biodiversity. An appropriate comment regarding exotic mammals was again made by Charles Darwin (1860) during his crossing of the Pampas and Patagonian landscapes

> "few countries [than Argentina] have undergone more remarkable changes since the year 1535, when the first colonist of La Plata

Table 1   Mammal harvesting in the Neotropical Region

Subsistence hunting[a]	Commercialization[b]	
Species	Species	1972–1978
Common Opossum	Nutria	11,011,288
Nine – banded armadillo	Gray Fox	5,789,011
Giant Armadillo	Opposums	1,541,717
Giant Anteater	Skunks	1,243,129
Lesser Anteater	Plains Vizcacha	820,177
Three-toed sloth	Geoffroy' s Cat	481,333
Two-toed Sloth	Guanaco	443,655
Night Monkeys	Peccaries	312,115
Titi Monkeys	Red Fox	101,251
Capuchin Monkeys	Capybara	89,656
Howler Monkeys	Pampa's Cat	82,195
Spider Monkeys	Puma	2571
Brazilian Cottontail	Total	21,918,098
Squirrels		
Agouti		
Capybara		
Common Tapir		
White-lipped Peccary		
Collared Peccary		
Brocket Deer		
Coatí		
Kinkajou		

[a]Most common mammals for subsistence hunters (adapted from Redford and Robinson, 1991).
[b]Mammal species and number of individuals (skins) exported legally from Argentina during 1972–1978 (data from Ojeda and Mares, 1982).

> landed with seventy-two horses. The countless herds of horses, cattle, and sheep, have altered the whole aspect of the vegetation, but they have almost banished the guanaco, deer, and ostrich. Numberless other changes must likewise have taken place; the wild pig in some parts probably replaces the pecari; packs of wild dogs may be heard howling on the wooded banks of the less frequented stream; and the common cat, altered into a large and fierce animal, inhabits rocky hills… ". (Charles Darwin, The Voyage of the Beagle, 1860, entry for September 19th, 1833)

The most impacted by invasions are the West Indian and Patagonian Subregions. Exotic mammals in South America represent about 20% of world mammal introductions, but the highest density of exotic mammals is found in the temperate Patagonian Subregion. Most introductions occurred in the eighteenth and nineteenth centuries, with more successful establishment in temperate ecosystems, between 34° and 55° S. They were facilitated by accidental introductions from ships of early explorers, or deliberate introductions in order to establish sport hunting or provide food and fur. Exotic Neotropical mammals include a variety of taxa (e.g., rodents, deer, wild boar, and mustelids), ecological groups (terrestrial and semiaquatic herbivores and carnivores, omnivores). Among the traits that were suggested for the success of invasive species are a high reproductive rate, large size of native geographic range, vacant niches, climatic matching, and so on (Novillo and Ojeda, 2009). Most species are of Eurasian origin and occupy similar ecoregions as in their native areas, although some have expanded their range of habitats. In Cabo de Hornos (55° S), for example, exotic species richness is higher

than that of natives. However, the understanding of the impacts of invasive mammals in the temperate region remains largely anecdotal for many of them (Jaksic et al., 2002; Novillo and Ojeda, 2009).

Approaches and Strategies for Conservation in a Heterogeneous Region

The Neotropical Region includes a diverse and complex mosaic of macrohabitats. **Figure 7** depicts large-scale species richness (=number of species) and level of endemism in South America. Despite the well-known diversity of the Amazon rainforest, the pattern in **Figure 7** highlights the importance of mammal diversity and endemism in non-amazonian dryland biomes (Mares, 1992). One of these is the semiarid thornscrub forests of the Gran Chaco, which covers more than 1 million km^2 across Paraguay, Bolivia, Argentina,

and Brazil. It possesses a rich fauna of medium- and large-sized mammals equivalent to some of the richest tropical rainforests (Redford et al., 1990). Other important dryland biomes are Mediterranean scrublands, Cerrado, Patagonian steppe, high Andean Altiplano, and Monte desert. Some of these, such as the Mediterranean shrublands and the Chaco, are poorly protected in existing reserves. Further, the plains of the Gran Chaco are currently undergoing a rapid and extensive process of transformation driven by conversion to soybean production (Zak et al., 2008).

Conservation of Neotropical mammals has been approached at various scales and political levels. Scales range from entire assemblages to populations and from major hotspots (e.g., Mesoamerica) to ecoregions or areas of particular interest (e.g., transitional zones between Neotropical subregions). Political approaches have been at the national level
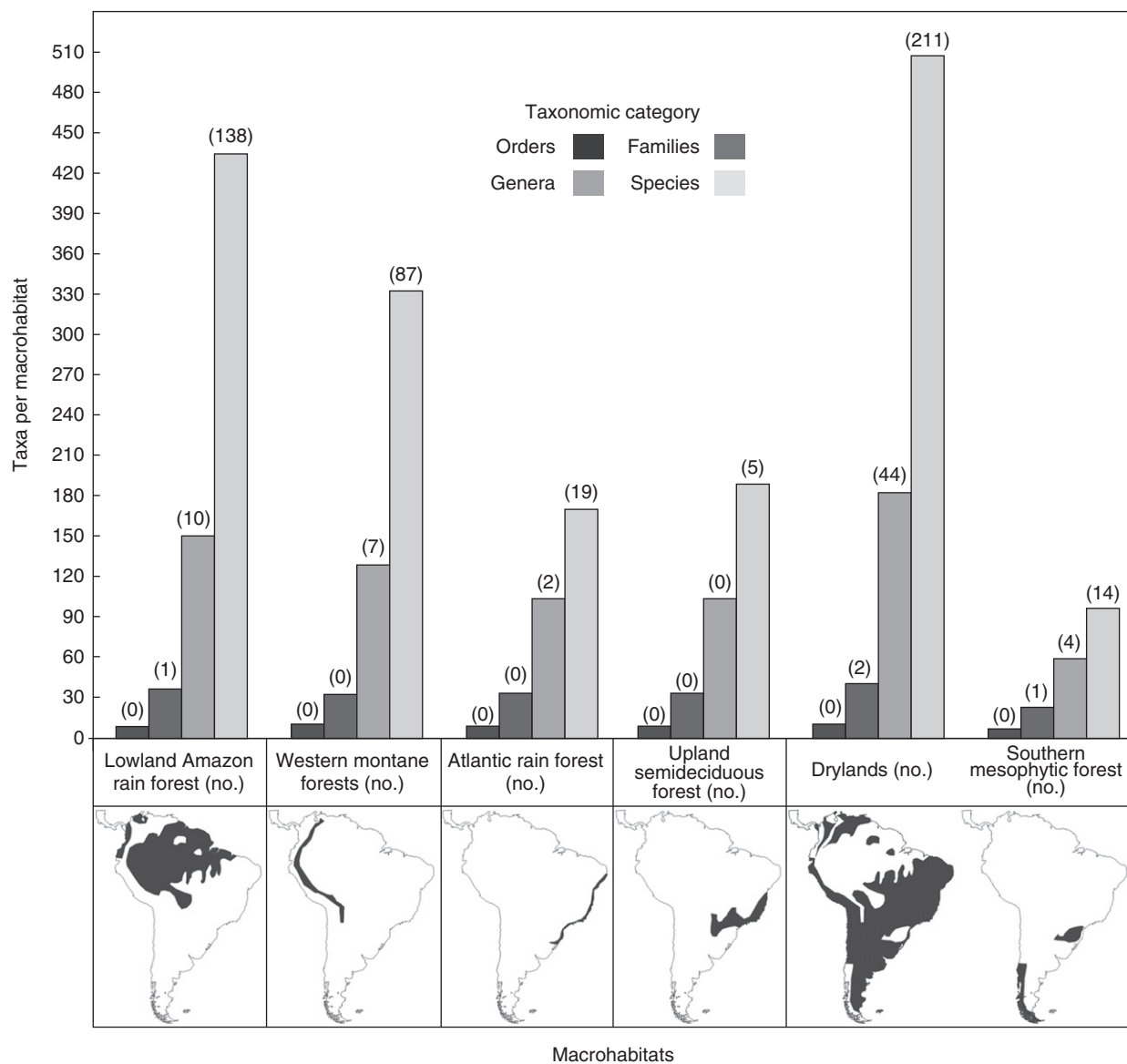

Figure 7 Mammal richness (orders, families, genera, and species) and endemisms in major South American macrohabitats. These macrohabitats differ in size (i.e., area) and the number of species they support is directly related to their area.

down to smaller subdivisions (e.g., provinces). Biodiversity hotspots, i.e., areas which combine extraordinary levels of endemism with low proportions of remaining original habitat, are important in planning and prioritizing mammal conservation at a global scale. The Neotropical Region includes seven hotspots in Central and South America. Among them are the tropical Andes, one of the most diverse regions on Earth. Other hotspots include the Caribbean, which retain 11.3% of their primary vegetation, and the Brazilian Atlantic Forest, with less than 10% of the original habitat. The other hotspots are the Cerrado (the second largest biome in Brazil), the Valdivian temperate rainforests of Chile, and the Tumbes-Chocó-Magdalena wetlands (stretching from Panama to Peru). (Myers et al., 2000; http://www.biodiversityhotspots.org).

Despite their potential value, most hotspots are incongruent when considering several biodiversity attributes such as species richness, endemism, and extinction threats. Consequently, there is a need for complementary approaches that incorporate conservation priorities and establishment of reserves and networks.

A useful alternative approach to hotspots is the use of ecoregions. Ecoregion divisions are based on classical biogeography and provide a finer resolution in assessing biodiversity. They can be used as a tool for conservation of species, habitats, and ecological processes of the ecoregion under study (http://www.worldwildlife.org/science/ecoregions/delineation.html) (Olson et al., 2001).

At a country scale, reserve networks (i.e., areas representing the total number of species, endemic species, endangered species, and species with restricted distributions) provide contrasts for maintaining regional biodiversity. For example, in megadiverse Mexico, 82% of mammal species are represented in the reserve network, which covers a small portion (3.8%) of the country (Ceballos, 2007). In contrast, in temperate Chile, only a small fraction of the ranges of endemic threatened species are under protection of the reserve system (Cofré and Marquet, 1999; Tognelli et al., 2008).

Prioritizing conservation in areas with high species richness and large numbers of endemic and endangered species is difficult due to the limited geographic overlap in these attributes for any given area. An example of an heterogeneous region is the tropical–temperate transitional belt of the southern cone of South America, where faunal differences in a variety of biomes requires the addition of many complementary reserves to existing ones in order to protect 90% of the total number of mammal species (Ojeda et al., 2003). Overall, regional biogeographic and macroecological analyses of mammal composition, population abundance, degree of occupancy, endemicity, and endangerment across the diversity of ecoregions can provide a baseline for additional studies and the establishment of global conservation strategies such as a network of protected areas maximizing complementarity (i.e., protected areas are chosen with the goal of efficiently achieving representation of all species within a particular criteria, such as endemic species, rare species, and so on; Ceballos, 2007).

Prospects

Prospects for understanding the biogeography and conservation of Neotropical mammals are promising. This is not only because of the growing development and quality of georeferenced databases of mammalian distributions and geographic ranges (e.g., http://www.natureserve.org/infonatura/) which help address the Wallacean shortfall (i.e., lack of biogeographic data and its variability), but also because of progress in delineating taxonomic units (Linnean shortfall) and systematic relationships through the advance of genetic and molecular techniques (Lomolino, 2004). Further advances in software applications and sophisticated modeling techniques in spatial analysis of distributions (e.g., GLM, generalized linear models; niche models, as BIOCLIM, GARP, and so on) hold promise of further development for biogeography, conservation, and the macroecology of Neotropical mammals. Together, all of these developments are strengthening the scientific basis of biodiversity conservation and management policies at several geographic scales and political units. However, there is also a need for interdisciplinary *dialog* in order to integrate and build a stronger, more rigorous biogeographical approach, instead of isolated research programs (Brown, 2004). This includes the consolidation of the theoretical foundations of this interdisciplinary science, and making research in this area more useful and relevant to the many problems of rapidly changing human landscapes at a global scale.

The extraordinary biotic diversity and heterogeneous matrix of the Neotropics, one of the most diverse biogeographic regions of the world, is presently experiencing unprecedented threats to major habitats due to a wide array of rapidly expanding human pressures, particularly those associated with commodity production (e.g., impacts of habitat conversion for soybean farming in the Amazon Basin, Cerrado, Chaco, and Pantanal).

A concerted effort among different segments of society is necessary to conserve the enormous mammalian diversity of the region. Unless there is a restructuring process, within the political domain, to equilibrate the disparity among social, environmental, and economic dimensions, the biodiversity losses in the Neotropical Region could escalate rapidly in the near future in the face of rapidly accelerating threats.

Acknowledgments

Appendix

Courses

- Mammalogy
- Biogeography
- Conservation Biology

See also: Central America, Ecosystems of. Ecosystems of South America. Endangered Mammals. Hotspots. Latitudinal Gradients of Biodiversity. Loss of Biodiversity, Overview. Mammals, Biodiversity of. Mammals, Conservation Efforts for. Mammals (Late Quaternary), Extinctions of. Mammals (Pre-Quaternary), Extinctions of. Marine Mammals, Extinctions of. Megaherbivores. South American Natural Ecosystems, Status of

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